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Johansen, Ole Munch; Andersen, Dagmar Kappel; Ejrnaes, Rasmus; Pedersen, Morten Lauge

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1 Relations between vegetation and water level in groundwater dependent
2 terrestrial ecosystems (GWDTEs)

3 Ole Munch Johansen¹, Dagmar Kappel Andersen², Rasmus Ejrnæs³, Morten Lauge Pedersen^{1*}

4 ¹ Department of Civil Engineering, Aalborg University, Thomas Manns Vej 23, Aalborg, DK-9220, Denmark

5 ² Department of Bioscience, University of Aarhus, Vejlsovej 25, Silkeborg DK-8600, Denmark

6 ³ Department of Bioscience, University of Aarhus, Grenaaavej 12, Rønne DK-8410, Denmark

7 *Corresponding author: mlp@civil.aau.dk

8

9 ABSTRACT

10 Alkaline wetlands and fens are groundwater dependent, terrestrial ecosystems (GWDTEs) existing
11 throughout the temperate zone. They contain a large number of protected and endangered plant
12 species and their ecological status is threatened by insufficient groundwater quality and quantity.
13 However, management and conservation of fens are constrained by limited knowledge on the
14 relations between vegetation and measurable hydrological conditions. This study investigates the
15 relations between vegetation and water level dynamics in groundwater dependent wetlands in
16 Denmark.

17 A total of 35 wetland sites across Denmark were included in the study. The sites represent a
18 continuum of wetlands with respect to vegetation and hydrological conditions. Water level was
19 measured continuously using pressure transducers at each site. Metrics expressing different
20 hydrological characteristics, such as mean water level and low and high water level periods, were
21 calculated based on the water level time series. A complete plant species list was recorded in plots
22 covering 78.5 m² at each site. Community metrics such as total number of species and the number
23 of bryophytes were generated from the species lists and Ellenberg Indicator scores of moisture, pH
24 and nutrients were calculated for each site.

25 The water level correlates with the number of typical fen species of vascular plants, whereas
26 bryophytes are closer connected to the stable water level conditions provided by groundwater
27 seepage. The water level variability is proved to be a significant limiting factor for species diversity
28 in wetlands, which should be considered along with the fertility in order to access the habitat
29 quality. The study provides new insight in the water level preferences for GWDTEs which is highly
30 needed in the management and assessment of anthropogenic damage to these ecosystems.

33 **KEYWORDS**

34 Alkaline wetlands, hydrology, vegetation, Ellenberg indicator values

35

1 Introduction

Groundwater dependent, terrestrial ecosystems (GWDTEs) include a range of wetland types including fens, alkaline springs, dune slacks, wet meadows and in some situations also bogs and transition mires, which are of conservation concern in the temperate zone worldwide due to a high species diversity and presence of many endangered species (Van Diggelen et al. 2006, Wassen et al 2005). In heavily populated regions human uses of the groundwater resource is considered as a major threat to these sensitive plant communities (Van Diggelen et al. 2006). In Europe, the Water Framework Directive (WFD) prescribes that GWDTEs are identified, mapped and taken into consideration in the assessment of the availability and quality of groundwater. In practice, however, addressing the policies regarding conservation and GWDTEs remains problematic due to the lack of operational criteria for assessment of wetland status and thresholds above which damage is expected (Whiteman et al. 2010). Therefore, quantitative relations are needed between the hydrology and the ecological status of GWDTEs.

Plant communities of GWDTEs are especially vulnerable to hydrological changes; however, their dependency on groundwater seepage is only partially understood. A constant alkaline groundwater supply keeps sediments and pore water highly buffered and prevents acidification (Boomer and Bedford 2008b) and reduces the availability of phosphorus (Wassen et al. 2015). Furthermore, the groundwater inflow sustains a water level close to the land surface most of the year and waterlogged conditions prevent aeration of organic matter and, hence, limit acidification and nutrient mineralization (Almendinger and Leete 1998, Verhoeven et al. 1996). The limited nutrient and oxygen availability in the root zone prevents more competitive species from invading the habitat thereby reducing compositional change and maintaining a high species diversity (Kotowski

et al. 2006). When the topsoil is unsaturated, periodic filling of soil pores with rainwater may occur (Schot et al. 2004) and this further increases the risk of acidification and increased nutrient mineralisation (Grootjans et al. 1988). Infiltration of nutrient rich surface water e.g. following a flooding event may also result in increased nutrient availability (Beumer et al 2007, Banach et al. 2009, Cusell et al. 2015).

The water table dynamics greatly influence redox conditions which again control internal binding and release of phosphorus, which is considered the limiting nutrient in wetland ecosystems (Lucassen et al. 2005). The position of the water table is only indirectly connected to these controlling chemical processes, and it does not take into account the variability in capillary rise which is often pronounced in GWDTE soils. Schaffers and Sýkora (2000) showed that there is a stronger correlation between soil water content and vegetation than between water table depth and vegetation for a wide range of plant communities from dry to wet soils. However, under very wet conditions, as in GWDTEs, it is here argued that the water level is a better and more robust measure because it is easy to measure, highly comparable and representative for the area surrounding the measurement point.

Previous studies have revealed significant correlation between mean water table and the relative number of hydrophytes in dune areas, heathlands, bogs and fens in the Netherlands (Runhaar et al. 1997). Wheeler (1999) emphasizes the difficulties of finding clear patterns between species composition and water table gradients across sites due to the large spatial and temporal variability of the water table dynamics. There are studies showing significant correlations between vegetation and mean water table metrics, while other studies indicate that extreme events or the frequency and duration of water level fluctuations significantly influence the vegetation composition (Wheeler

1999). However, species typical of GWDTEs are known to be highly sensitive to increased nutrient availability (e.g. Bedford et al. 1999, Bergamini and Pauli 2001) and thus, considering the trophic status along with water table measures is necessary for a reliable assessment of status of these habitats (Andersen et al. 2013). In this study, continuous water level registrations between 2004 and 2010 are analysed to identify measures that correlate with the vegetation in 35 Danish GWDTEs. A high temporal resolution of water level data in the study makes it possible to derive statistical measures and test the correlation with vegetation composition. The objectives of the study can be summarised as follows:

- To investigate relations between water level metrics and characteristic vegetation in alkaline GWDTEs
- To establish quantitative models linking water level metrics to vegetation metrics which can be operationally useful in the management of alkaline GWDTE sites.

2 Materials and methods

Data from 35 GWDTEs located across the northern and eastern part of Denmark was analysed (Fig. 1). Of the 35 sites, 29 are classified as *alkaline fens* within the NATURA 2000 network. A categorisation of the remaining six sites was conducted by vegetation based classification according to the Habitats Directive (Ejrnæs et al. 2004; Nygaard et al. 2009). Three sites were thereby categorised as *alkaline fens*, one as *calcareous fens with Cladium mariscus and species of the caricion davallianae* and two as *molinia meadows on calcareous, peaty or clayey- silt-laden soils*. The occurrence of alkaline GWDTEs in the western part of Denmark is very limited due to flat

105 terrain, sandy soils, and absence of alkaline groundwater aquifers. Therefore, the spatial occurrence
106 of alkaline GWDTEs in Denmark is represented by the selected sites.

107

108 2.1 Water level

109 Water level data was collected using pressure transducers for continuous registration. Some systems
110 automatically compensate for barometric pressure, while others use a reference atmosphere
111 recording. The original water level series were sampled with varying density between 30 min and
112 24 h, and there were a few minor gaps in the data. All data was therefore averaged to continuous
113 time series of daily mean values. The time series were trimmed so that only whole years were used
114 and annual measures could be calculated correctly. Most data was collected as a part of the Danish
115 monitoring programme supplemented with four additional stations from other projects (Ejrnæs et al.
116 2010, Johansen et al. 2011).

117

118 Water level time series were analysed from each of the 35 sites in order to link water level metrics
119 and vegetation composition. The general approach used in ecology is to relate the water table to the
120 ground surface level. In some wetland habitats, the ground surface is, however, not easily defined
121 due to the micro-topographic variability. In order to obtain a base level for the water level we used
122 the stable winter water level as the base level. A stable water level near the terrain surface was
123 typically observed from November to April (Fig. 2). We calculated this base level as the 90 %
124 quantile of the water level time series and denoted H_{90} . For sites where the soil surface was
125 homogeneous and precise ground levels were obtained, the differences between H_{90} and the actual
126 ground level were found to be within a few centimetres. This approach is only applicable at sites
127 where the water table is close to or equal to the terrain surface during winter periods and without
128 long term inundation from a nearby stream or lake.

129

130 The overall minimum water level, H_{min} , was calculated as the minimum of all observed values,
131 which reflects the water level during the driest period recorded at the site. Different ways of
132 representing the water level variability is tested by the metrics H_{mean} , H_{20} , H_{IQR} (definitions are given
133 in Table 1). The Dry_{dur} is the share of time where the water table is more than 50 cm below the base
134 level (H_{90}). Previous vegetation studies primarily deal with spring or summer water levels.
135 Therefore, we calculated the mean water level in the periods April-June ($H_{mean \text{ Apr.-Jun.}}$) and July-
136 August ($H_{mean \text{ Jul.-Aug.}}$). To evaluate the effect of a rapidly changing water table, the mean water level
137 variance over periods of three days throughout July and August (Var_3) was calculated. Table 1
138 summarises all water level metrics.

139

140 2.2 Vegetation

141 The vegetation data constitutes complete species lists recorded in one 78.5 m² plot (circle with
142 radius = 5 m) on each of the 35 sites. On 19 sites, the vegetation plots were centred on the
143 corresponding water level well, while on the remaining sites we used similar vegetation
144 registrations from the Danish monitoring programme from the plot closest to the well; the distance
145 ranging from 2-60 metres.

146

147 The typical species used for evaluation of conservation status were masked from a list published by
148 Ejrnæs et al. (2009). The list contains potential typical species of alkaline wetlands, fens and
149 springs, which are referred to in the Habitats Directive (European Commission 1992) and the
150 corresponding CORINE biotopes (European Commission 1991). The list was further supplemented
151 with species from Nordic habitats (Påhlsson 1994) referred to in the Interpretation manual
152 (European Commission 2007). Species, which do not predominantly occur in alkaline fens or

153 springs were excluded from the list (See appendix A, Table A.1 for the total species list). We added
 154 the list of species used in this study because it makes it possible to compare with future studies.
 155
 156 For each site, the vegetation data were used to calculate average Ellenberg Indicator values. The
 157 Ellenberg indicator system is an expert system that is partly based on measured data, but mainly on
 158 expert knowledge and experience of the optimal environmental conditions for single plant species
 159 (Ellenberg et al. 1991, Wamelink et al. 2002). Ellenberg values were averaged over all species
 160 present in a plot and were used as surrogate for measured environmental conditions (Diekmann
 161 2003). The Ellenberg indicator system has a score for nitrogen (*EN*) in the range of 1-9, which
 162 describes the nutrient availability and potential productivity. An *EN* value of 1 indicates extremely
 163 infertile sites and a score of 9 indicates extremely nutrient-rich conditions. The Ellenberg R value
 164 (*ER*) indicates soil reaction and ranges from 1 to 9 where 1 is extreme acidity and 9 indicates basic
 165 reaction only found on high pH soils. Ellenberg F (*EF*) is the moisture indicator between 1 and 12
 166 where 1 is an indicator of extremely dry sites and 12 represent permanently submerged plants.
 167 Throughout the study, we used Ellenberg indicator values calibrated to the British flora (Hill et al.
 168 1999). Danish studies have shown that the ratio between the parameters *EN* and *ER*, also referred to
 169 as the “nutrient ratio”, correlates particularly well with the number of typical species in Danish,
 170 alkaline fens and springs (Andersen et al. 2013).
 171
 172 Table 2 shows the vegetation parameters used in the study. The number of typical species (*T*) is
 173 used as a measure of habitat conservation status (Andersen et al. 2013). However, a large scatter in
 174 the link between typical species and the water level was expected. Therefore, it was examined
 175 whether or not correlations would improve by excluding typical species with $EF < 8$ in the metric
 176 T_{wet} . Bryophytes are more directly dependent on a shallow water table than vascular plants, due to

the lack of vascular tissue for the transport of water from greater depths. The total number of bryophytes (B), the typical bryophytes (TB) and the relative number of bryophytes (B_{rel}) were also used as metrics to characterise the bryophyte community. The highest observed number of typical bryophytes in the study was only 7, which is problematic when trying to obtain highly significant correlations. The total number of species (S_{tot}) and the relative number of hydrophytes (H_{rel}), based on EF scores, provide alternative metrics based on all observed species. Finally, the mean Ellenberg indicator values EN , ER , EF and the ratios $EN\ ER^{-1}$ and $EN\ EF^{-1}$ were included as metrics in the analyses.

2.3 Relations between water level and vegetation

Spearman rank correlation coefficients (Rho) were calculated between all combinations of hydrological metrics (Table 1) and the vegetation metrics (Table 2) along with the probability of the two parameters being uncorrelated (P_{val}).

Plotting vegetation metrics against the four water level metrics (H_{min} , H_{IQR} , H_{mean} and Dry_{dur}), quantile regression analysis was used to test the consistency of tendencies by subdividing the x-axis into seven categories and finding the highest scoring sites within each of these subdivisions. Fitting a line through the seven highest scoring points, the intersection with the x-axis represents the point where vegetation scores are zero due to limitation by hydrological conditions, whereas the intersection with the y-axis represents the point where water level is not a limiting factor.

Further, multivariate Poisson regression techniques were applied to model the species diversity as a function of water level metrics and additional explanatory variables. The purpose was to explain some of the expected residual variation in the regressions. The Poisson distribution was assumed to

201 be valid, since the response variable (number of species) is a small but non-negative integer value.
 202 The statistics toolbox in MATLAB was used to conduct the analysis. The Poisson regression model
 203 expresses the log outcome as a linear function of a set of predictors:
 204

$$\log(\mu) = \eta = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k \quad (1)$$

205 where μ is the mean of the response variable and η is the linear combination of the coefficients β_i
 206 and the independent variables x_i so that
 207

$$\mu = \exp(\eta) \quad (2)$$

208
 209 In order to analyse the residuals of the initial regression models two additional Poisson regression
 210 models linking Ellenberg indicators and hydrological metrics were established. Model 1 predicts the
 211 number of typical species, and model 2 predicts the number of bryophytes. Both models are based
 212 on the mean water level in July-August ($H_{mean Jul.-Aug.}$) and nutrient ratio ($EN ER^{-1}$) as explanatory
 213 variables. In combination with the nutrient ratio, $H_{mean Jul.-Aug.}$ is the hydrological metric provided
 214 the best prediction.
 215

216 This yields following expressions for the applied models based on equations (1) and (2):
 217

$$Model\ 1: T_{pred} = \exp\left(b_0 + b_1\left(\frac{EN}{ER}\right) + b_2\left(H_{mean Jul.-Aug.}\right)\right) \quad (3)$$

218

$$Model\ 2: B_{pred} = \exp\left(c_0 + c_1\left(\frac{EN}{ER}\right) + c_2(H_{mean\ Jul.-Aug.})\right) \quad (4)$$

219

220 T_{pred} and B_{pred} are the predicted number of typical species and bryophytes respectively. The
 221 coefficients \bar{b} and \bar{c} are determined by linear regression.

222

223 3 Results

224 3.1 Water level and vegetation dataset

225 Within the 35 sites, registration of water level started in 2004 while the main part of the dataset only
 226 covers the period 2007 to 2009. The average length of the water level time series is 3.5 years, but
 227 only five months are overlapping (30 June 2008 to 4 Dec 2008) between all stations. The eastern
 228 and western parts of the country are equally well-represented by the data for all years.

229

230 3.2 Relations between water level and vegetation metrics

231 The correlation between the total number of typical species, T , and the hydrological measures was
 232 significant on a 5 % level for 6 of 8 water level metrics. The highest direct correlation with typical
 233 species was obtained for H_{IQR} ($Rho = -0.38^*$) while correlations with the short term variability
 234 (Var_3) and spring mean ($H_{mean\ Apr.-Jun.}$) were insignificant. As expected, the number of bryophytes
 235 were closer related to the hydrology than vascular plants with highly significant ($p < 0.01$)
 236 correlations with all water level metrics. Also for bryophytes, H_{IQR} showed the highest correlation
 237 ($Rho = -0.54^{**}$). The number of typical species and bryophytes decrease with increasing annual
 238 amplitude in water level.

239

240 The Ellenberg moisture indicator (EF) correlates significantly with all water level metrics, however,
241 EF is by far closest related to the short term variability expressed by Var_3 ($Rho = -0.68***$). The
242 highest correlation between a water level metric and a vegetation metric was obtained between the
243 inner quartile range of the water level H_{IQR} and the relative number of bryophytes B_{rel} ($Rho = -$
244 $0.69***$). The relative number of bryophytes was, furthermore, very closely related to the ratio
245 between the Ellenberg nutrient and moisture indicators $EN\ EF^{-1}$ ($Rho = -0.79***$). All spearman
246 rank correlation coefficients and P-values between quantitative metrics (Table 1 and Table 2) are
247 listed in appendix B, Table B.1.

248

249 At high and stable water levels the observed habitat quality expressed as the number of typical
250 species ranges from poor to high (left on all graphs, Fig. 3), while at the dry sites (right on all
251 graphs, Fig. 3), the number of typical species is always low indicating that water level is a limiting
252 factor. For all four vegetation metrics such limitation occurs when the minimum water level (H_{min})
253 is around 1.5 m. A good agreement on this point was found between different vegetation metrics.
254 Across different water level metrics the location of the intersection with the y-axis did not change
255 much either. So despite a large scatter in the relations between vegetation and water level there
256 seems to be a clear upper limit to all vegetation metrics which is constrained by water level
257 conditions.

258

259 A considerable scatter in the water level vegetation relations was found (Fig. 4). The *nutrient ratio*
260 ($EN\ EF^{-1}$) has been shown to correlate well with the number of typical species and, hence, this
261 nutrient indicator may explain some of the residual variation in the regressions of typical species
262 and bryophytes against hydrological metrics. Based on the models in Fig. 5, we found bryophytes to

263 be more dependent on a high and stable water table than the typical species collectively. The
264 explanatory value of the mean water level was highly significant in model 1 ($p < 0.01$) and very
265 highly significant in model 2 ($p < 0.001$). In both cases, the nutrient ratio explained a larger share of
266 the variance than the water level (Table 3 and Table 4). The results of applying multivariate
267 regression to predict the number of typical species (model 1) and bryophytes (model 2) are shown
268 in Fig 5.

269 4 Summary and discussion

270 The study comprised 35 alkaline GWDTEs located throughout Denmark, thus comprising a
271 representative sample of Danish GWDTEs with respect to hydrology and vegetation composition.
272 We found significant relationships between the number of typical fen species and 6 out of 8
273 hydrology metrics and highly significant relationships between water level metrics and the number
274 of bryophyte species, while bryophyte species richness decreases with increasing annual water level
275 amplitude. The established models confirmed that bryophytes are more dependent on a high and
276 stable water level than vascular plants.

277
278 The proposed models (3) and (4) indicate a change in the number of typical species by a factor 2
279 and a change in the number of bryophytes by a factor 3 corresponding to the observed range of
280 water level. This applies to sites where the presence of species and hence diversity is primarily
281 limited by water level conditions. Comparable results have been reported elsewhere (Duval et al.
282 2012) and Ilomets et al. (2010) conclude that the number and cover of fen species decreases sharply
283 when the seasonal water level fluctuations exceed 25 cm within the Paraspõllu calcareous-rich fen
284 in northern Estonia. Our proposed models can be used as tools for evaluating the conservation status
285 and determining the limiting factor for species diversity in Danish GWDTEs. The models can also

286 predict the expected changes in species diversity due to changes in water level conditions. Care
287 must be taken when interpreting the results. The underlying assumption is that water level and
288 nutrient availability are independent parameters. For small seasonal changes in water level, the
289 assumption can be valid, but for large water level fluctuations the nutrient availability is likely to
290 change significantly as a consequence of internal eutrophication (Almendinger and Leete 1998,
291 Verhoeven et al. 1996) and changing redox conditions (Boomer and Bedford 2008a, Boomer and
292 Bedford 2008b) at least until a new equilibrium state has been established.

293

294 The strongest correlation ($Rho = 0.68$) for the Ellenberg moisture indicator *EF*, was found with the
295 short term water level variability in the summer period (Var_3). The short term variability is highly
296 dependent on soil texture, where permeable clayey soils show a higher amplitude of water level
297 fluctuations during summer periods compared to that of highly permeable sandy soils. Ertsen et al.
298 (1998) have shown that non-linear relationships between *EF* and water level apply best to clayey
299 soils while linear relationships provide the best fit for peaty and sandy soils. However, the
300 individual soil classes did not improve the amount of variance explained in their models. Our results
301 indicate that the *EF* score is related closer to the short term water level dynamics and soil texture
302 than to the mean annual or mean seasonal water level metrics. The number of typical species and
303 the number of bryophytes are, on the other hand, not closely related to this short term variability,
304 but rather to the annual or seasonal dynamics. An additional explanation to the poor correlation
305 between typical species and *EF* is that species preferring wet conditions occur along the entire
306 gradient of nutrient status. Species typical of alkaline fens and springs may share a general
307 preference of wet conditions. However, the range in nutrient availability is limited to the low end of
308 the nutrient gradient. These results are in agreement with the results of Andersen et al. (2013),
309 where a similar weak correlation between typical fen species and *EF* was found.

310

311 Wet conditions clearly result in a larger share of bryophyte species compared to vascular plant
312 species as indicated by the highly significant relationships between the water level measures and the
313 relative number of bryophytes B_{rel} . The relative number of bryophytes is closely related to
314 Ellenberg N, and in particular the ratio between Ellenberg N and Ellenberg F. In other words, the
315 number of bryophytes becomes prominent when the conditions are wet and nutrient poor. This is in
316 agreement with the results of Mälson and Rydin (2007), who found that bryophytes disappeared
317 from alkaline fen areas shortly after drainage, and several studies have shown inhibition or
318 competitive disadvantage with increased nutrient availability (Bergamini and Pauli 2001, Kooijman
319 2012, Andersen et al. 2016) or even toxic effects of especially ammonium on fen bryophytes
320 (Paulissen et al. 2004, Verhoeven et al. 2011).

321

322 A strong, positive correlation between EN (nutrient score) and ER (pH score) was demonstrated for
323 the sites in this study. This acidity-alkalinity gradient from bogs to rich fens is often interpreted as a
324 nutrient availability gradient with associated changes in species richness and productivity caused by
325 changes in nutrient availability (Bedford et al. 1999). The fen species typically depend on low
326 values of EN and high values of ER . Both EN and ER correlate positively with the magnitude of
327 seasonal water table fluctuations. The positive correlation between EN and low water table can be
328 caused by oxygen penetrating the soil, followed by an internal release of nutrients due to soil
329 mineralisation or by an input of groundwater low on cations thereby reducing immobilisation of
330 phosphorus (Boomer and Bedford 2008a, Niedermeier and Robinson 2009). On the other hand
331 phosphorus is more effectively bound to iron when periodic aeration of the peat occurs (Lucassen et
332 al. 2005, Smolders et al. 2006). There is no commonly accepted explanation to the positive
333 correlation between ER and water table fluctuations. It is, however, well known that a number of

334 processes such as sulphur oxidation and nitrification decrease alkalinity when oxygen is available
335 while sulphate reduction and denitrification increase alkalinity when no oxygen is available
336 (McLaughlin and Webster 2010). However, as the water table fluctuations increase so does the
337 oxygen availability which should then lead to acidification (Van Haesebroeck et al. 1997). A
338 possible explanation to this could be that evaporative effects increase the concentration of minerals.
339 Large seasonal fluctuations in the water table are due to the evapotranspiration being larger than the
340 groundwater inflow during dry spring and summer periods. Excessive rainfall during fall and winter
341 brings the water level close to the terrain surface again. This in turn leads to increased
342 concentrations of dissolved minerals including Ca-ions and thereby increases in alkalinity. So,
343 groundwater inflow provides the minerals that prevent acidification of fens, however, the largest
344 alkalinity could be present for low-intermediate groundwater fluxes where evapotranspiration
345 becomes important. Another possible explanation of the positive correlation between ER and water
346 table fluctuations may be the strong positive correlation between *ER* and *EN* ($Rho = 0.76$). In that
347 respect, the correlation possibly reflects a shift in vegetation towards more competitive species, than
348 a shift towards a more alkaline environment.

349

350 5 Conclusions

351 The water level correlates with the number of typical fen species, whereas bryophytes are closer
352 connected to the stable water level conditions provided by groundwater seepage. We found
353 significant relationships between the number of typical fen species and 6 out of 8 hydrology metrics
354 and highly significant relationships between water level metrics and the number of bryophyte
355 species. Bryophyte species richness decreases with increasing annual amplitude in water level
356 fluctuations. The established models confirmed that bryophytes are more dependent on a high and
357 stable water level than vascular plants.

358

359 The strongest correlation for the Ellenberg moisture indicator EF, was found with the short term
360 water level variability in the summer period (Var3). The relative number of bryophytes is closely
361 related to Ellenberg N, and in particular the ratio between Ellenberg N and Ellenberg F.

362

363 Our proposed models can be used as tools for evaluating the conservation status and determining
364 the limiting factor (nutrients or hydrology) for species diversity in Danish GDWTEs. The relative
365 number of bryophytes to total species is very closely related to water level conditions, which can be
366 useful in situations where no or limited water level data is available. The models can also predict
367 the expected changes in species diversity due to changes in water level conditions. The water level
368 variability is proved to be a significant limiting factor for species diversity in GDWTEs,
369 emphasizing the importance of considering optimal hydrology along with the fertility in order to
370 access the habitat quality.

371

373

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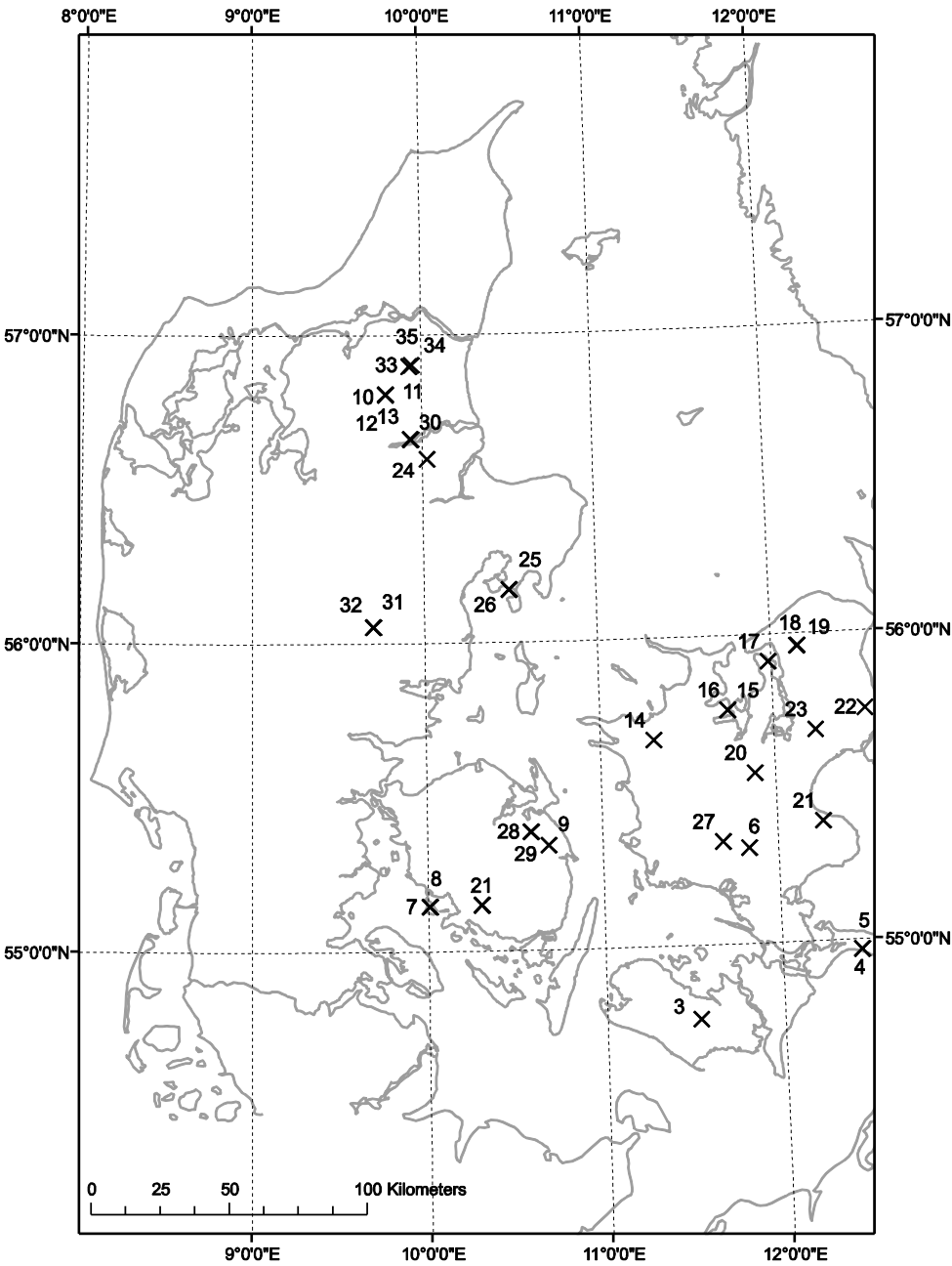
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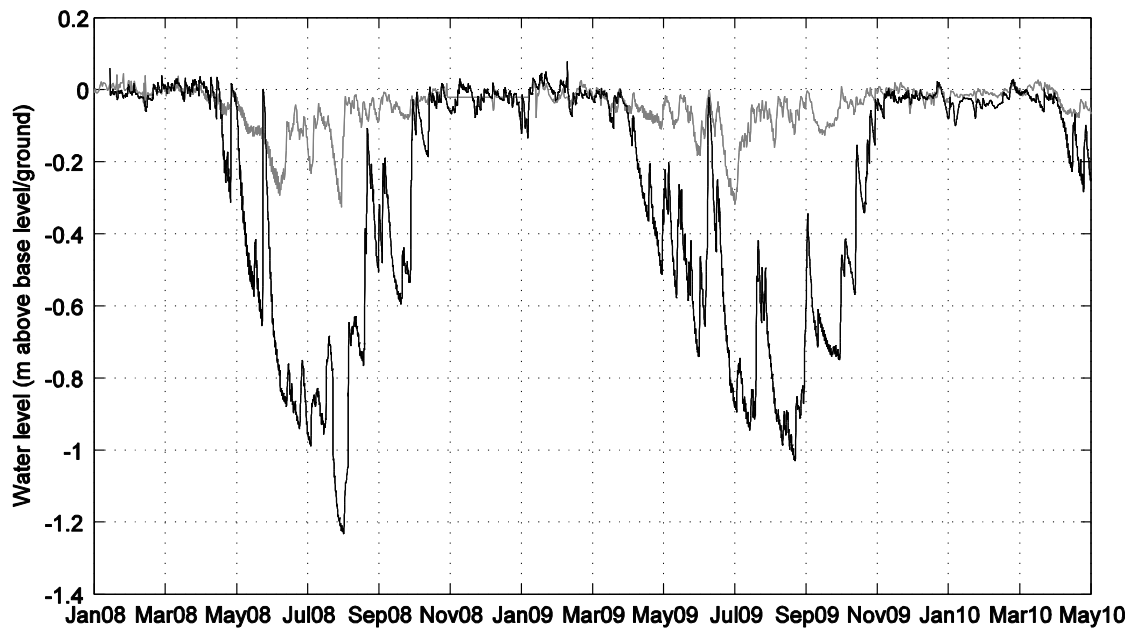
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487 Fig. 1 Location of the 35 sites concentrated in northern and eastern Denmark.
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491 Fig. 2 Example of water level time series analysed. The grey line represent a site with a minor
 492 lowering of the water table in the summer period, and the black line represent a site with a more
 493 dynamic summer water table.

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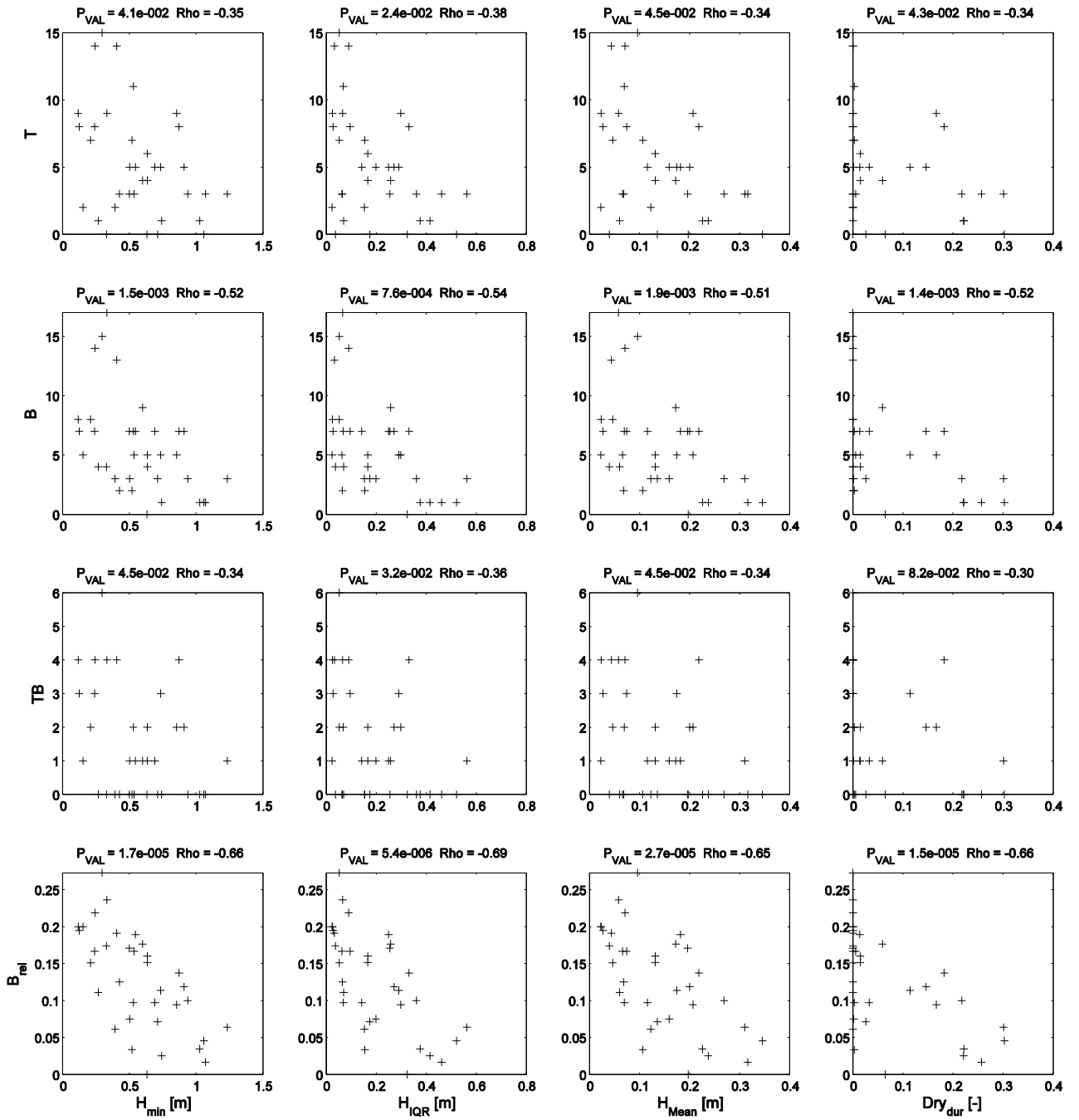


Fig. 3. Four vegetation measures T , B , TB , B_{rel} plotted against four water level measures H_{min} , H_{IQR} , H_{mean} , Dry_{dur} . Rho and P_{val} based on Spearman's rank correlation is shown

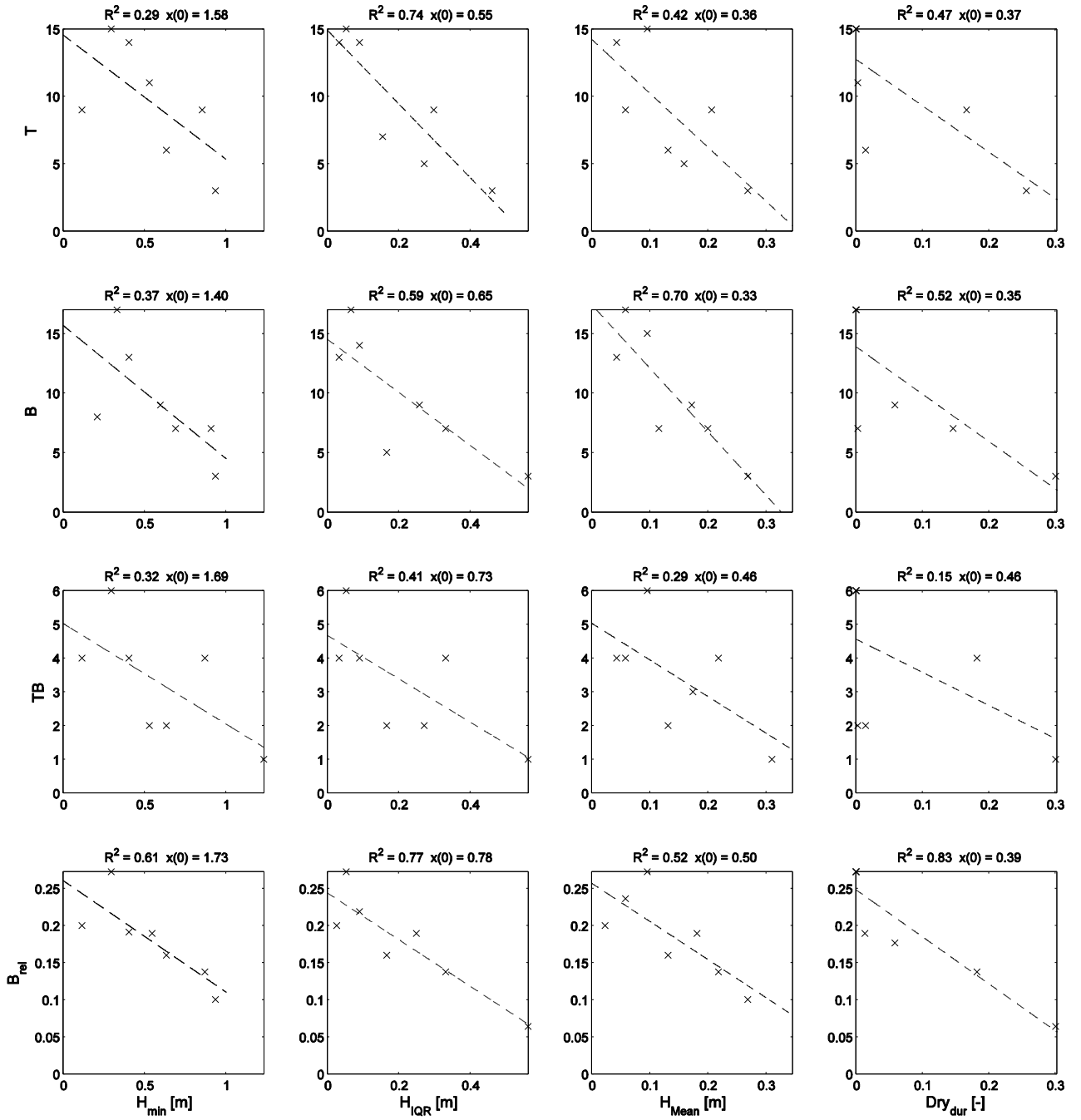
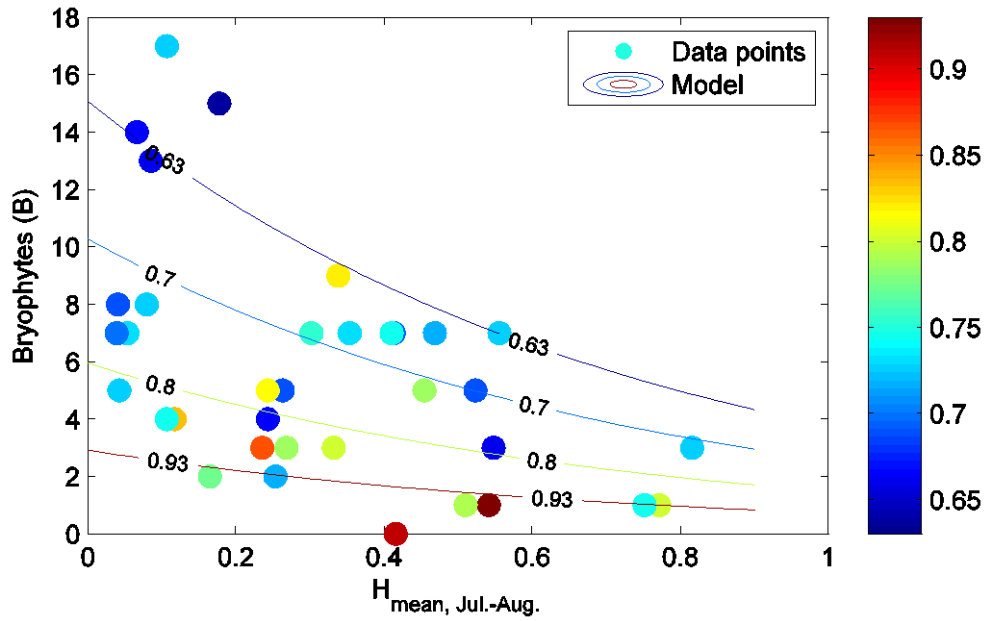
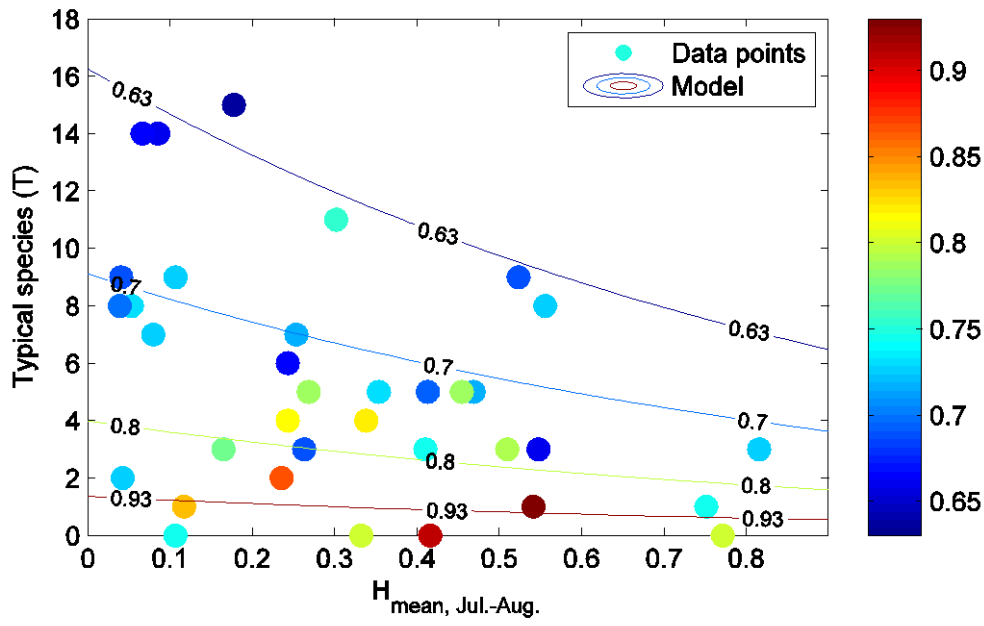


Fig. 4. The highest scoring point along seven subdivision of the x-axis each containing 5 observation points. The dashed line represents a linear model of these maximum values with the shown R^2 value and intersect with the water level axis equal to $x(0)$



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Fig. 5. Visualisation of Poisson regression model 1 (upper) and model 2(lower) using a Poisson distribution for the predicted variables T and B . The contour lines are values of the nutrient ratio EN ER^{-1} . The original data points are shown with respect to the x-axis and y-axis.

512 **TABLES**

513

514 Table 1. Statistical measures calculated from water level time series and observed ranges at study
515 sites

Symbol	Unit	Observed range	Definition
H_{min}	m	0.12 – 1.23	H_{90} - lowest observed water level
H_{mean}	m	0.02 - 0.35	H_{90} - Mean observed water level
H_{20}	m	0.04 - 0.73	H_{90} - Water level drawdown exceeded 20 per cent of the time
H_{IQR}	m	0.02 - 0.56	H_{75} - H_{25} , Inner quartile range of water level
Dry_{dur}	%	0-30 %	$H < (H_{90} - 50 \text{ cm})$, relative duration of period with more than 50 cm to the water table
$H_{mean \text{ Apr.-Jun.}}$	m	0.02 - 0.40	H_{90} - mean observed water level in April to June
$H_{mean \text{ Jul.-Aug.}}$	m	0.04 - 0.82	H_{90} - mean observed water level in July to August
Var_3	m	7e-5 - 8e-3	Mean variance evaluated over periods of 3 days during July and August

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520 Table 2. Vegetation parameters: examined and observed ranges at study sites.

Symbol	Unit	Observed range	Definition
T	Number	0-15	Number of typical species
T_{wet}	Number	0-6	Number of typical species where Ellenberg F (moist) score ≥ 8
B	Number	0-17	Number of bryophytes
TB	Number	0-6	Number of typical bryophytes
B_{rel}	%	0-27	Relative number of bryophytes
S_{tot}	Number	16-72	Total number of species
H_{rel}	%	18-74	Relative number of all species with Ellenberg F score ≥ 8
EN	Score	3.5-6.0	Mean Ellenberg N (nutrient) score
ER	Score	4.9-6.4	Mean Ellenberg R (pH) score
EF	Score	5.9-8.2	Mean Ellenberg F (moist) score
$EN\ ER^{-1}$	Ratio	0.63-0.93	Ratio between EN and ER - the “nutrient ratio”

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526 Table 3. Statistics of model 1 using a Poisson distribution for the predicted variable

Typical species	Coefficient estimates	Std. error of b	p-value of b
	b		
b_0 (intercept)	8.00***	0.99	4.8e-16
b_1 Ellenberg N/R	-8.27***	1.40	3.1e-9
b_2 $H_{mean, Jul.-Aug.}$	-1.02**	0.38	7.5-e-3

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529 Table 4. Statistics of model 2 using a Poisson distribution for the predicted variable

Bryophytes	Coefficient estimates	Std. error of c	p-value of c
	c		
c_0 (intercept)	6.16***	0.89	4.4e-12
c_1 Ellenberg N/R	-5.47***	1.25	1.2e-5
c_2 $H_{mean, Jul.-Aug.}$	-1.39***	0.38	2.4e-4

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533 Appendix A

534 Table A.1 Typical species of alkaline springs (S) and rich fens (F) (Ejrnæs et al. 2009), number of
 535 presences as typical species in other EU- member states and frequency of occurrence in current
 536 study. Species marked by grey colour are excluded due to more frequent occurrence in other
 537 habitats in Denmark. Bryophytes are marked by bold.

Species	Habitat	Corine /other	EU-presences	Occurences in current dataset (35 plots)
Aneura pinguis	S	Corine 54.251, 54.54.52, 54.541, Nordisk min.3.4.2.1	4	2
Briza media	F		0	10
Bryum pseudotriquetrum	S, F	Corine 54.2, Nordisk min.3.4.2.1	9	11
Calliergonella cuspidata	S	Corine 54.4, Nordisk min.3.4.2.1	1	32
Campylium protensum	F	(Corine 54.2 “and others”)	0	3
Campylium stellatum	S, F	Corine 54.2, 54.23	8	9
Cardamine amara	S	Corine 54.113	1	0
Carex dioica	F	Corine 54.25	10	1
Carex hostiana	F	Corine 54.2	6	1
Carex lepidocarpa	F	Corine 54.121, 54.2	8	5
Carex nigra	F	Corine 54.23	0	21
Carex pulicaris	F	Corine 54.21	4	2
Carex viridula	F	Corine 54.2 (c. flava)	7	3
Cratoneuron filicinum	S	Corine 54.12, Nordisk min.3.4.2.1	13	7

Ctenidium molluscum	F	Corine 54.2	2	1
Dactylorhiza incarnata	F	Corine 54.2	6	3
Dicranum bonjeanii	F	Nordisk min. 3.5.2.3	0	2
Eleocharis quinqueflora	F	Corine 54.2, 54.23	14	1
Epipactis palustris	S, F	Corine 54.2, 54.23	14	9
Equisetum telmateia	S	Corine 54.12	1	0
Eriophorum angustifolium	F	Corine 54.4	1	10
Fissidens adianthoides	F	Corine 54.2, Nordisk min.3.4.2.1	6	3
Hypericum tetrapterum	S		0	5
Juncus articulatus	S	Corine 54.23	0	21
Juncus inflexus	S	Nordisk min.3.4.2.1, (corine 37.241, 37.242)	1	0
Juncus subnodulosus	F	Corine 54.2, Nordisk min.3.4.2.1	12	11
Limprichtia cossonii	S, F	Corine 54.2, 54.23, Nordisk min.3.4.2.1	2	3
Liparis loeselii	F	Corine 54.2	7	1
Lychnis flos-cuculi	S, F		0	15
Menyanthes trifoliata	S, F	Corine 54.422	0	8
Montia fontana ssp. fontana	S	Corine 54.111	0	0
Nasturtium microphyllum	S	Corine 53.4	0	0
Nasturtium officinale	S	Corine 53.4	0	0
Palustriella commutata	S	Corine 54.12, Nordisk min.3.4.2.1	16	0
Palustriella falcata	S	Corine 54.12, Nordisk	3	0

min.3.4.2.1				
Parnassia palustris	F	Corine 54.21, 54.23	10	1
Pedicularis palustris ssp. palustris	F	Corine 54.422	0	4
Philonotis calcarea	S	Interpret. manual 7220,(corine 54.2 ”and others..”)	13	0
Philonotis fontana	S	Corine 54.111	2	0
Pinguicula vulgaris	S, F	Corine 54.12, 54.2, 54.23	10	0
Potentilla erecta	F	Corine 54.23	0	11
Ranunculus flammula	S	Corine 54.422	0	12
Rumex acetosa ssp. acetosa var. Hydrophilus	S		0	0
<i>Sphagnum teres</i>	F	Nordisk min. 3.4.3.2, (Nordisk min. 3.4.1.3)	2	2
Sphagnum warnstorffii	F	Nordisk min. 3.4.2.1, , 3.4.3.2	0	0
Stellaria alsine	F	(corine-spring 54.113),	0	0
<i>Succisa pratensis</i>	F	Corine 37.31	0	11
Tomentypnum nitens	S, F	Nordisk min. 3.4.2.1, 3.4.3.2	4	4
Triglochin palustris	S, F		4	11

Appendix B

Table B.1 Spearman rank correlation coefficients (upper right) and p-values (lower left) for all combinations of water level and vegetation measures. n.s. is not significant

($p > 0.05$)

	<i>Rho</i>	Vegetation measures												Water level measures							
<i>Pval</i>		<i>T</i>	<i>T_{wet}</i>	<i>B</i>	<i>IB</i>	<i>B_{rel}</i>	<i>H_{rel}</i>	<i>S_{tot}</i>	<i>EN/ER</i>	<i>EN/EF</i>	<i>EF</i>	<i>EN</i>	<i>ER</i>	<i>H_{min}</i>	<i>H_{IQR}</i>	<i>H₂₀</i>	<i>H_{mean}</i>	<i>Dry_{dur}</i>	<i>H_{mean}</i> <i>Apr.-Jun.</i>	<i>H_{mean}</i> <i>Jul.-Aug.</i>	<i>Var₃</i>
Vegetation measures	<i>T</i>		0.84	0.76	0.87	0.53	0.33	0.61	-0.65	-0.39	0.32	-0.33	0.10	-0.35	-0.38	-0.35	-0.34	-0.34	-0.31	-0.37	-0.23
	<i>T_{wet}</i>	2E-10		0.65	0.63	0.43	0.49	0.54	-0.44	-0.40	0.44	-0.29	-0.02	-0.36	-0.34	-0.33	-0.31	-0.40	-0.29	-0.35	-0.33
	<i>B</i>	2E-7	3E-5		0.80	0.83	0.33	0.50	-0.53	-0.55	0.36	-0.46	-0.26	-0.52	-0.54	-0.53	-0.51	-0.52	-0.45	-0.49	-0.45
	<i>IB</i>	1E-11	5E-5	8E-9		0.63	0.23	0.47	-0.55	-0.31	0.24	-0.22	0.16	-0.34	-0.36	-0.35	-0.34	-0.30	-0.31	-0.37	-0.25
	<i>B_{rel}</i>	1E-3	1E-2	7E-10	4E-5		0.43	0.02	-0.57	-0.79	0.47	-0.64	-0.45	-0.66	-0.69	-0.66	-0.65	-0.66	-0.61	-0.66	-0.58
	<i>H_{rel}</i>	n.s.	3E-3	6E-2	n.s.	1E-2		-0.12	-0.14	-0.52	0.95	-0.14	-0.10	-0.47	-0.36	-0.34	-0.35	-0.42	-0.40	-0.48	-0.65
	<i>S_{tot}</i>	1E-4	7E-4	2E-3	4E-3	n.s.	n.s.		-0.18	0.14	-0.15	0.04	0.18	0.00	-0.02	-0.02	-0.01	-0.04	0.04	0.00	0.10
	<i>EN/ER</i>	2E-5	8E-3	1E-3	6E-4	4E-4	n.s.	n.s.		0.71	-0.10	0.80	0.28	0.22	0.36	0.31	0.28	0.23	0.22	0.26	0.05
	<i>EN/EF</i>	2E-2	2E-2	7E-4	n.s.	2E-8	1E-3	n.s.	2E-6		-0.52	0.88	0.67	0.56	0.65	0.61	0.59	0.59	0.56	0.57	0.49
	<i>EF</i>	n.s.	8E-3	3E-2	n.s.	4E-3	9E-19	n.s.	n.s.	1E-3		-0.11	-0.07	-0.51	-0.41	-0.39	-0.40	-0.45	-0.45	-0.50	-0.68
	<i>EN</i>	n.s.	n.s.	5E-3	n.s.	3E-5	n.s.	n.s.	7E-9	2E-12	n.s.		0.76	0.35	0.50	0.45	0.43	0.43	0.36	0.35	0.16
	<i>ER</i>	n.s.	n.s.	n.s.	n.s.	7E-3	n.s.	n.s.	n.s.	1E-5	n.s.	1E-7		0.35	0.47	0.46	0.45	0.46	0.38	0.33	0.20
level	<i>H_{min}</i>	4E-2	3E-2	1.5E-3	5E-2	2E-5	4E-3	n.s.	n.s.	4E-4	2E-3	4E-2	4E-2		0.89	0.89	0.89	0.96	0.86	0.94	0.84

	H_{IQR}	2E-2	5E-2	7.6E-4	3E-2	5E-6	4E-2	n.s.	3E-2	3E-5	2E-2	2E-3	5E-3	1E-12		0.99	0.98	0.89	0.93	0.92	0.65
	H_{20}	4E-2	n.s.	1.1E-3	4E-2	1E-5	4E-2	n.s.	n.s.	1E-4	2E-2	6E-3	5E-3	6E-13	1E-27		1.00	0.88	0.95	0.93	0.64
	H_{mean}	5E-2	n.s.	1.9E-3	5E-2	3E-5	4E-2	n.s.	n.s.	2E-4	2E-2	1E-2	7E-3	7E-13	2E-25	8E-36		0.88	0.95	0.93	0.64
	Dry_{dur}	4E-2	2E-2	1.4E-3	n.s.	2E-5	1E-2	n.s.	n.s.	2E-4	6E-3	1E-2	5E-3	5E-19	2E-12	3E-12	6E-12		0.82	0.91	0.79
	$H_{mean\ Apr.-Jun.}$	n.s.	n.s.	6.4E-3	n.s.	9E-5	2E-2	n.s.	n.s.	4E-4	7E-3	3E-2	2E-2	3E-11	3E-16	1E-17	3E-18	1E-9		0.92	0.70
	$H_{mean\ Jul.-Aug.}$	3E-2	4E-2	2.6E-3	3E-2	1E-5	4E-3	n.s.	n.s.	4E-4	2E-3	4E-2	n.s.	6E-17	2E-15	5E-16	3E-16	2E-14	3E-15		0.76
	Var_3	n.s.	n.s.	7.3E-3	n.s.	2E-4	3E-5	n.s.	n.s.	3E-3	6E-6	n.s.	n.s.	2E-10	3E-5	3E-5	4E-5	1E-8	2E-6	1E-7	